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The adaptiveness of a queuing strategy shaped by social experiences during adolescence

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ABSTRACT

Social experiences during adolescence profoundly influence behavioural and endocrine phenotypes. A key question is whether these environmentally induced changes can adjust the individual to prevailing environmental conditions. Previous work shows that male guinea pigs living in pairs from early adolescence are more aggressive and exhibit distinctly higher cortisol responses than males living in large mixed-sex colonies. In environments with limited numbers of competitors, the high-aggressive phenotype of pair-housed males (PMs) leads to more dominant positions and higher reproductive success compared with colony-housed males (CMs) and thus represents an adaptation to this situation. Here we tested whether CMs, conversely, are better adapted to the complex social life in large groups. For that purpose, pairs of one PM and one CM were placed into large mixed-sex colonies during late adolescence. During the initial days, PMs displayed significantly more aggressive behaviour than CMs. Nevertheless, PMs and CMs achieved only low dominance ranks and did not reproduce at that time. Simultaneously, PMs showed marked increases in testosterone and cortisol as well as substantial reductions in body weight, whereas CMs coped with the situation in a non-stressful way. A few days later, however, PMs changed their high-aggressive strategy to a low-aggressive queuing strategy and could no longer be distinguished from CMs. As a consequence, PMs and CMs did not differ in numbers of sired offspring. In summary, these results demonstrate that adolescence is a sensitive phase not only for adapting to current environmental conditions but also for readjusting phenotypic development when the actual environment deviates from earlier predictions.

1. Introduction

Behavioural development can be profoundly shaped by environmental influences during ontogeny, which enables organisms to adapt to the prevailing conditions [31,49]. Such adaptive developmental plasticity does not necessarily provide an immediate advantage but may prepare individuals for conditions they are likely to encounter in later life, as described by the concept of predictive adaptive responses [4]. Phenotypic development is particularly susceptible to external stimuli during prenatal and early postnatal phases, by which environmental cues are often transmitted from parents to offspring [19,29].

More recently, adolescence has been recognised as another important life stage for adjusting development in response to environmental conditions [11,38,39]. The adolescent life stage encompasses the gradual transition from childhood to adulthood and is associated with complex alterations in brain structures, endocrine systems and behaviour [6,44,45]. As sexual maturation emerges, social interactions increasingly occur in the context of reproductive competition. Particularly in mammals, adolescents become independent and often leave their natal group [45], so that they typically encounter unfamiliar environmental conditions and conspecifics. Moreover, the developing individuals receive information about the environment directly, rather than being mediated largely via the parents. Hence, adolescence may provide an additional opportunity for adaptively shaping the phenotype and for readjusting development when prevailing conditions deviate from earlier predictions [39].

There is a growing body of research demonstrating remarkable long-term effects of the adolescent environment on behaviour and neuroendocrine functioning in mammals and birds [6–8,10,34,47]. Some of these plastic responses have been considered to represent adaptations to particular environmental conditions. In rats, for example, adolescent social defeat seems to prepare males for effectively coping with comparable social challenges in later life [7]. Furthermore, exposure to chronic unpredictable stress during adolescence leads to a negative cognitive bias in adulthood, which has been interpreted as a potential risk aversion in adjustment to dangerous environments [8]. The clearest

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evidence to date for an adaptive shaping of the phenotype by environmental influences during adolescence has recently been provided in guinea pigs [51]. When housed in mixed-sex pairs from early adolescence, males are characterised by considerably higher levels of aggression towards other males and greatly enhanced courtship activities in presence of unfamiliar females compared with males housed in large mixed-sex colonies during the same time [18,41]. In addition, pair-housed males show significantly greater cortisol responses to various challenging situations compared with colony-housed males [18,24,41]. These differences seem to be brought about by an interaction of behavioural and neuroendocrine processes, through which social experiences trigger testosterone secretion [25]. In turn, testosterone levels have organisational effects on cortisol responsiveness during adolescence [23], which consequently appears to influence the regulation of social behaviour [39].

The different phenotypes are assumed to be part of reproductive strategies that represent adaptations to environmental conditions associated with different population densities [38,39]. The high-aggressive phenotype seems beneficial in environments with limited numbers of competitors, in which fighting for a dominant position and defending mating opportunities likely improves reproductive success. Conversely, it appears that the low-aggressive strategy of queuing is advantageous for the complex life in large social groups, as it helps to avoid reproductive competition until developing males are large enough to effectively challenge other males for mating access. Such density-dependent reproductive strategies have also been described for the ancestor of the guinea pig, the wild cavy, in its natural habitat, where individual numbers can greatly fluctuate within relatively short periods of time [2,3]. At low population densities, these animals live in male-female pairs or, more rarely, in small single-male groups including two females [3]. In contrast, at high population densities, single-male groups including up to three females are more common and may additionally comprise developing males displaying an alternative reproductive strategy of queuing [2]. The shaping of different behavioural phenotypes by the respective adolescent experiences has thus probably evolved as an adaptive response to these varying social conditions [39].

However, compelling evidence for the adaptive significance of the adolescent shaping process requires a full factorial experimental design, in which individuals of both housing conditions are reciprocally exposed to the different situations [13,28]. In a first step, we recently confirmed that pair-housed males indeed have a fitness benefit when competing with a single colony-housed male of the same age for mating access [51]. Consistent with previous work [18,41], pair-housed males were significantly more aggressive towards the opponent and showed distinctly higher levels of courtship and sexual behaviour than colony-housed males in this situation. This high-aggressive strategy was accompanied by substantial increases in circulating cortisol as well as testosterone and rapidly led to a dominant position, which ultimately translated to higher reproductive success [51].

The aim of the present study was to determine the adaptive value of the phenotypic adjustment during adolescence by completing the full factorial design. Accordingly, we elucidated whether the low-aggressive queuing strategy confers a fitness benefit under complex group-living conditions and investigated the underlying endocrine mechanisms. For that purpose, pairs of one pair-housed and one colony-housed male were placed into large mixed-sex groups of unfamiliar conspecifics during late adolescence following sexual maturation, where we examined their social behaviour, endocrine responses, changes in body weight and reproductive success. Due to their different social experiences earlier in adolescence, it was assumed that pair-housed males would be more aggressive and show higher levels of courtship and sexual activities than colony-housed males. Correspondingly, we expected larger increases in plasma concentrations of cortisol and testosterone in pair-housed males compared with colony-housed males. However, in agreement with the environmental matching hypothesis, we predicted that the high-aggressive strategy would be less successful than the low-aggressive queuing strategy and eventually lead to lower reproductive success.

2. Material and methods

2.1. Animals and housing conditions

The guinea pigs were housed in four mixed-sex colonies, each kept in an enclosure of approximately 6 m^2 and consisting of 7–12 males, 11–16 females and their pre-weaned offspring (< 3 weeks of age). Both sexes showed a graduated age structure ranging up to 20 months. At 30 (± 1) days of age, 24 male subjects, each from a different litter, were assigned to pair-housing or colony-housing conditions. Each pair-housed male was placed together with an unknown female in an enclosure of 0.5 m^2. Colony-housed males were transferred to an unfamiliar colony. Allocation to the different housing conditions was balanced for body weight. All animals were housed under standard conditions: 12:12 LD cycle, temperature 22 ± 2 °C, relative humidity 50 ± 15%. Commercial guinea pig diet and water were available ad libitum. See Lürzel et al. [24] for further details.

All procedures complied with the EU Directive 2010/63/EU on the protection of animals used for scientific purposes and were approved by the local and national authorities (LANUV; reference number: 84–02.05.20.12.117).

2.2. Experimental design and procedures

At 120–125 days of age (i.e. in late adolescence, about 1–2 months after reaching sexual maturity), one pair-housed and one colony-housed male were simultaneously placed into an unfamiliar colony to examine behavioural performance, endocrine responses and reproductive success of the individuals. Experimental design and schedule of assessments are depicted in Fig. 1. The males were introduced at 09:00 h (± 15 min) and social interactions were scored immediately after transfer on day 1 and on days 2, 3, 8 and 15 in the new environment. Collections of blood samples and determinations of body weights were performed 20 h before transfer (day 0), 4 h after transfer on day 1 as well as on days 2, 3, 8 and 15. The interval between consecutive introductions of male subjects into the same colony was at least three

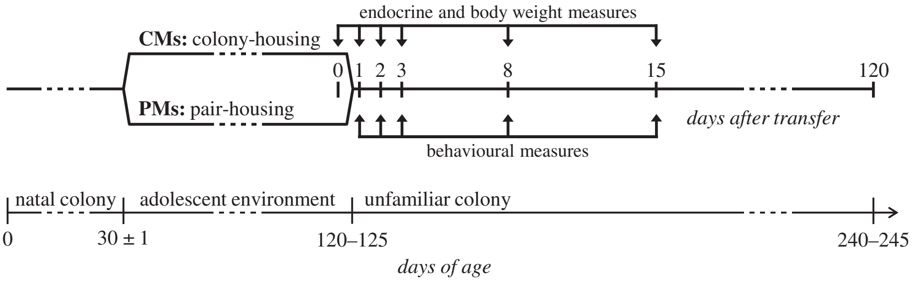

Fig. 1. Experimental design and schedule of assessments. Colony-born males were transferred to different adolescent social environments at 30 (± 1) days of age and subsequently housed either in another colony (CMs) or pairwise with one female (PMs). At 120–125 days of age (i.e. in late adolescence), pairs of one pair-housed male and one colony-housed male were placed into unfamiliar colonies for up to 120 days (n = 12). Plasma cortisol and testosterone concentrations and body weights were determined 20 h before transfer (day 0), 4 h after transfer on day 1 and on days 2, 3, 8 and 15 after transfer. Social interactions were scored during the first 190 min after transfer on day 1 and for 2 h each on days 2, 3, 8 and 15 after transfer.